Diet and Incisor Surface Curvature in Cercopithecids

Research Thesis

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by

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Abstract

Understanding the relationship between tooth morphology and feeding ecology in extant taxa provides for more reliable interpretations of the primate fossil record. Recent studies by Deane (2005, 2008, 2009) suggest that frugivorous species, especially hard-object feeders, have incisors of relatively greater labial and mesio-distal curvature than folivorous species. The present study builds on the work of Deane and that of Schubert et al. (2010) to further test the relationship between diet and incisor surface curvature in an expanded sample of African cercopithecids.

Maxillary central and lateral right incisors of adults were measured in a sample representing ten cercopithecid genera and eleven species for which dietary information was available. Each taxon was assigned to one of three diet categories. Points were recorded at one-millimeter intervals along the surface using a measuring microscope. Polynomials were then fit to the data and the first derivative of the line tangent to the curve at each point was determined. Logistic regression analysis on the first derivatives was used to test the ability of incisor curvature to predict diet type.

Results indicate that, based on incisor curvature, individuals could be correctly assigned to their respective diet categories more than 73% of the time when two groups were compared at a time. However, when the mean slopes of the lines tangent to the curve were compared there appeared to be little difference among the three groups, indicating there may be no discernable difference in incisor curvature among the categories used. More data on food material properties as well as on the mechanics of incising different food types are necessary to test associations between curvature and diet and to determine the functional significance of incisor curvature. Only then can we know if this element of incisor shape can be used to infer diet in fossil taxa.

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Introduction

Diet is a fundamental aspect of an animal's ecological niche and there has long been interest in the functional relationships between diet and primate tooth form (e.g., Hrdlička, 1920). Dental morphology has been found to reflect the wide range of primate diets in many ways and can be used to make inferences about diet in fossil taxa (Kay, 1984). Most of this research, however, has explored molar morphology while the functional role of incisors is much less understood. Past studies have looked at the size (Hylander, 1975), feeding behavior (Ungar, 1994a), microwear (Ungar, 1994b), orientation (Ang et al., 2006), and breadth and wear (McCollum, 2007) of incisors. These studies will be further discussed but the concern of the present study is incisor curvature, an aspect of incisor morphology only recently under investigation.

Previous Studies of Incisor Curvature

The present study builds on the work of Deane et al. (2005), who described a new method of quantifying anatomical curvatures: high-resolution polynomial curve fitting (HR-PCF). He argues that this method differs from other methods of measuring curvatures because it can be applied to non-circular curvatures, such as tooth curvatures and many other anatomical curvatures, and to incomplete bones or teeth, meaning it is applicable to fossil fragments. In HR-PCF, the outline of an element is simplified and digitized (Figure 1) and, using software specifically designed for HR-PCF, the pixels making up the selected portion of the outline, the curvature of interest, are used as data points to fit a second-degree polynomial to the curve. The coefficients of the polynomial are the raw data to be used for statistical analysis.

Deane et al (2005) used HR-PCF to investigate the relationship between incisor curvature and broad dietary categories in extant hominoids. They used three dental crown marginal angles and two open contours (labial and mesio-distal) for I^1, I^2, I_1, and I_2 of seven hominoid species (74 individuals) and had nine variables per tooth (values of the three angles plus the coefficients from the second-degree polynomials of the two open contours). The hominoids were separated into three categories based on available dietary information: hard-object frugivore, soft-object frugivore, and folivore. They used discriminant function analysis to successfully differentiate between the three groups and found that I^1 and I^2 were the best teeth for discriminating among the groups. They also found greater I^1 mesio-distal and I^2 labial curvature in hard and soft-object frugivores compared to folivores and that hard-object frugivores had greater I^1 mesio-distal curvature than soft-object frugivores. Soft-object frugivores and folivores, however, had greater curvature in the mesio-distal dimension of the I^2 than hard-object frugivores.

Further studies by Deane (2009a) used a much larger sample of extant hominoids (295 individuals), this time divided into four categories: hard-object frugivore, soft-object frugivore, dedicated folivore, and mixed folivore/frugivore. Measurements of maximum mesio-distal length and labio-lingual breadth were recorded and mesio-distal and labial curvature data were obtained using HR-PCF. He found that 86.8% of individuals could be correctly assigned to dietary categories and that all frugivores relative to mixed folivore/frugivores and dedicated folivores had incisors of greater mesio-distal width and of greater labial and mesio-distal curvature (Figure 2). I^1, I^2, and I_1 were more mesio-distally curved and I^1, I_1, and I_2 were more labially curved. Furthermore, he found hard-

object frugivores to have more mesio-distally curved I^1 and I_2 and more labially curved I_2.

Deane (2009b) then applied his methods to a sample that included extant hominoids and early Miocene fossil catarrhines and examined the curvature and linear dimensions tooth by tooth. He found that the fossil taxa generally had less curved I^1 in both dimensions compared to the extant taxa but were most similar to the mixed folivore/frugivore group. *Afropithecus turkanensis* was an exception among the fossil taxa and was more closely associated with the hard and soft-object frugivores. For the I^2, the fossil taxa appear to be intermediate in mesio-distal curvature between the dedicated folivores and the mixed folivore/frugivores and soft and hard-object frugivores. Comparisons of I_1 suggest that the majority of the fossil taxa fall among the frugivores, with *Afropithecus turkanensis* falling more in the direction of the mixed folivore/frugivores and dedicated folivores and having the least curvature of all taxa. For the I_2, fossil taxa are more closely associated with the mixed folivore/frugivores and dedicated folivores. Overall, with the exception of *Afropithecus turkanensis*, all of the fossil taxa in this sample had less curved incisors in both dimensions, indicating that they were more folivorous. This interpretation is consistent with the fact that they also had narrower mesio-distal length relative to labio-lingual breadth, which has been suggested to be evidence of folivory (Harrison, 1993). Here, Deane has demonstrated that incisor curvature carries a strong signal for diet among extant hominoids and can be applied to fossil taxa to infer diet.

Most recently, Deane (in press) investigated the incisor curvature-diet relationship in another primate clade, the platyrrhines. This time he divided 133 individuals into three

groups: folivory, frugivory/omnivory, and sclerocarp foraging. The results were that sclerocarp foragers had increased I^1 and I^2 labial and mesio-distal curvature relative to all others and that curvature of I^2 was greater in both dimensions in frugivore/omnivores than in folivores. This study suggests the potential for a functional association between incisor curvature and diet throughout the primate order.

Cercopithecids

Building on this previous work, Schubert et al. (2010) tested whether incisor curvature differed among species of a third primate group, the cercopithecidae. These authors classified 87 individuals into two broad categories based on clade and diet: colobines/folivory and cercopithecines/frugivory. Their methods differ from HR-PCF in two main ways: (1) measurements of curvature were taken using a measuring microscope, with points at one-millimeter intervals as data points for the curve rather than pixels, and (2) mean slopes of the curves were the compared using logistic regression analysis. They suggested that cercopithecines/frugivores had greater I^1 labial mean slopes and greater I^2 mesio-distal mean slopes than colobines/folivores. Individuals could be assigned to the correct dietary category/clade 78.16% of the time but there was no attempt to distinguish between hard and soft fruit eaters.

The Present Study

The present study expands the Schubert et al. (2010) cercopithecid sample in terms of both the number of individuals and the number of species. The taxa are divided into three broad dietary categories: (1) hard-object diet, (2) mixed diet, and (3) soft-object diet. Based on findings of previous studies, predictions are that individuals can be correctly assigned to their respective diet categories based on the degree of incisor

curvature and that hard-object feeders will have the greatest degree of incisor curvature and soft-object feeders will have the least degree of incisor curvature, with the mixed diet group intermediate.

Methods

Measurements were taken from male and female adult right I^1 and I^2 casts created from specimens at the American Museum of Natural History and the National Museum of Natural History. Any specimens showing significant wear or damage were excluded. The sample includes 188 individuals from 10 cercopithecid species (Table 1). The species were divided into three groups based on dietary information in the literature. Group One, the hard-object feeders, includes the following two species: *Cercocebus torquatus* and *Macaca nemestrina* (Caldecott, 1986, Mitani, 1989). Group Two, the mixed-diet feeders, includes the following three species: *Lophocebus albigena*, *Papio anubis*, and *Procolobus badius* (Whiten et al., 1991, Maisels et al., 1993, Lambert et al., 2004, Okecha and Newton-Fisher, 2006). Group Three, the soft-object feeders, includes the following five species: *Cercopithecus mitis*, *Chlorocebus aethiops*, *Erythrocebus patas*, *Nasalis larvatus*, and *Trachypithecus cristatus* (Roonwal and Mohnot, 1977, Whitten, 1983, Cords, 1986, Bennett and Sebastian, 1988, Yeager, 1989, Brotoisworo and Dirgayusa, 1991, Isbell, 1998, Isbell et al., 1998).

Using a measuring microscope, points were recorded at one-millimeter intervals along both the labial curvature (from the cemento-enamel junction to the incisal edge) and mesio-distal curvature (from the midpoint of the mesial edge to the midpoint of the distal edge) on the surface of right I^1 and right I^2 (Figure 3). The measurements were adjusted so that the endpoints were positioned at 0 on the x-axis. SAS was used to

determine the best fitting equation, ranging from second-order to fourth-order polynomials, for each curve with an R^2 value of 95% or higher.

Total tooth length was divided into nine equal sections yielding eight points, excluding the beginning and ending points of the total length, to account for the fact that teeth vary in size. Using the 1st derivative of each equation the slope of the line tangent to each of the eight points was found and the mean slopes were compared at each point for each species. Logistic regression analysis was used to test whether species could be correctly assigned to their respective dietary categories based on the mean slopes with the greatest variation. Then the mean slopes at each point on each tooth were compared to determine which group had the greatest degree of incisor curvature.

Results

The mean slopes of greatest variation are listed in Table 2. Using these values, individuals were correctly assigned using logistic regression analysis to either Group One or Group Two 77.3% of the time, Group Two or Group Three 73.4% of the time, and Group One or Group Three 74.6% of the time (Table 3).

When the mean slopes at each point were plotted (Figures 4-7) it was evident that the mean slopes of greatest variation found using logistic regression analysis also show the greatest variation here, but differences among the three groups, in general, are not readily apparent. This is because the greatest mean slopes occur not in one group but in each of the three groups at seemingly random points. The mean slopes for each group are very similar at most points.

Discussion

In our sample, certain points on the curves could fairly accurately distinguish between hard-object feeders, soft-object feeders, and species with mixed diets and while it is tempting to interpret this as significant, none of the groups appears to have mean slopes increasing or decreasing more rapidly than either of the other groups on any curve of any tooth. This means there is no discernable difference in the degree of either labial or mesio-distal incisor curvature of I^1 or I^2 among any of the three groups. These findings do not reflect those of Deane et al. (2005), Deane (2009a, 2009b, in press), or Schubert et al. (2010).

There are a number of reasons why our results may not mirror those of previous studies. First, the sample size was likely a factor in the ambiguity of the results not only because the entire sample is only 188 individuals, but also because there is a far greater number of soft-object feeders than of either hard-object feeders or those with mixed diets. Ideally, future studies will expand the sample so that each group is equally represented.

Second, neither the present study nor that of Schubert et al. (2010) restricts analysis to second-degree polynomials. HR-PCF requires that only second-degree polynomials be used. Deane et al. (2005) explain that this is because higher degree polynomials impose points of inflection and are very sensitive to irregularities on the surface of the tooth, potentially altering the simple curve or including unimportant anomalies. Here we used second to fourth-order polynomials with $R^2 \geq 95\%$ while it may be wise to use only second-order polynomials with $R^2 \geq 85\%$ as in the HR-PCF method.

Third, the fact that these results are not in accord with those of previous studies may be because there is no association between broad diet categories and incisor

curvature in cercopithecids. This seems unlikely, given that previous studies have found strong associations in hominoids and platyrrhines, but it is possible.

Finally, the three diet categories are quite broad because the available dietary information is limited and only allows for the construction of broad categories. These categories may not reflect the complexity of species' dietary niches. Information about the specific material properties (e.g., toughness, hardness) of foods and about how teeth are used is necessary in order for a better understanding of the forces at work in different contexts during food processing activities; i.e., how teeth of differing degrees of curvature are interacting with the material properties of foods primates are consuming. This issue would affect not only the present study but also many studies of dental morphology and diet. This will be discussed further below.

A Functional Mechanism for Incisor Curvature

Assuming sample size or method errors are not factors, the results of this study do not show an association between incisor curvature and diet in this sample of cercopithecids; however, a functional mechanism for incisor curvature is still an issue of concern. Deane et al. (2005) and Deane (2009a, 2009b, in press) all suggest strong associations between incisor curvature and diet, yet the underlying mechanism remains unknown. Deane (2009a) acknowledges that developing hypotheses concerning diet in relation to significant variation in tooth morphology is difficult due to the lack of information about the material properties of the foods being processed. He does make some preliminary hypotheses to be tested when necessary data are available.

Deane (2009a) notes that species that eat foods that are both hard and tough have more pronounced mesio-distal curvature. He suggests that since hard food items subject

teeth to increased occlusal loading, greater mesio-distal curvature increases the occlusal surface area on which forces are applied during ingestion. Conversely, taxa that consume softer diets have lesser degrees of mesio-distal curvature because they experience lesser loading regimes and do not require greater surface area. In addition, straighter occlusal surfaces may be better for gripping or tearing foliage in more folivorous taxa. Deane (2009a) argues that a more folivorous diet requires the least mesio-distal curvature and hard-object feeding requires the most mesio-distal curvature, with soft-object frugivores having intermediate degrees of curvature, because of the mechanical demands related to food hardness.

Deane (2009a) also discusses the fact that all frugivores generally have greater labial curvature. He hypothesizes that this is a result of bending stresses in the antero-posterior plane while fracturing hard fruits and then removing the inner pulp; increased labial curvature resists bending farther from the neutral axis of the crown. Another possibility is that labial curvature, when combined with mesio-distal length and labio-lingual breadth, may increase crown cross-sectional area, thus increasing overall resistance to loading. Folivores and soft-object feeders who have lesser labial curvatures may have so because occlusal loading from the diet they consume is not substantial enough to require increased resistance to bending or increased cross-sectional area.

While increasing length and breadth will result in increased occlusal surface area or cross-sectional area, it is not readily apparent how increased curvature would contribute to increases in these aspects. Testing these hypotheses would involve the development or modification of models similar to those described by Ang et al. (2006) and Plavcan and Ruff (2008), discussed below. The shape of the lingual side of the

incisor has not been considered. Whether or not this aspect of the tooth follows a curvature similar to that of the labial side will affect both the occlusal surface area and the cross-sectional area of the tooth. Further, any issues with tooth wear were not addressed.

Deane understands that identifying the functional mechanism for incisor curvature requires information about the material properties of foods. This means quantifying specific hardness and toughness values representing the wide range of foods that primates eat. What many studies investigating associations between diet and tooth morphology, including the present study, fail to do is represent the complexity of species' dietary niches and the wide range of ingestive behaviors (Figure 8). There has been a tendency to oversimplify the relationships between diet and tooth form by placing taxa into broad categories based on the predominant food type in their diet or based on taxonomy when the physical properties of foods may be more important in terms of ecological challenges (McGraw and Daegling, In press). In order for studies such as this to reflect the complexity of dietary-morphological relationships, tooth curvature needs to be examined apart from taxonomic associations and dietary classifications and both the material properties of foods and the behavioral aspects of ingestion (e.g., Yamashita, 2003) need to be considered.

A History of the Study of Incisors

In order to assess future directions for the study of incisors it is important to understand and evaluate what has been done and what we know about different aspects of incisor morphology. Here, a few key studies are highlighted and a brief history of the study of primate incisors is discussed.

Hylander (1975) investigated associations between the length of the incisor cutting edge and diet in a large sample of catarrhine species and two platyrrhines species. He defined length as the distance between the distal edge of the cemento-enamel junctions of the left and right lateral incisors, both upper and lower. He plotted and fit a regression line to the mean values of these measurements for each species against body mass and found that, among the cercopithecids, most cercopithecines fell above the regression line while most colobines fell below the line, meaning that the cercopithecines had greater anterior tooth size in this dimension than the colobines. While dietary information for all species was not available at this time, Hylander was able to show that frugivorous species (the majority of cercopithecines) had greater anterior tooth size than folivorous species (the majority of colobines). The cercopithecines that fell below the lines were taxa that ate grasses (e.g., *Theropithecus*) or small foods, such as berries, (e.g., *Erythrocebus*) rather than large fruits, and the colobines that fell above the line tended to eat more fruit (*Colobus badius*). He found similar results for the hominoids and platyrrhines in the sample.

Hylander's (1975) reasoning for the variation in anterior tooth size was that primates that eat foods that require extensive incisal preparation (i.e., tearing, cutting, removal of tough coverings, etc. prior to ingestion of large, tough-skinned fruits) will experience more abrasion than those which eat foods that do not require the same extent of incisal preparation (i.e. leaves, berries, small seeds, flowers, grasses, etc.). Greater incisor size is therefore an adaptation to wear and serves to delay tooth damage.

Later studies stood somewhat in contrast to Hylander's findings. McCollum (2007) investigated incisor wear and breadth in *Pan troglodytes troglodytes* and *Gorilla*

gorilla gorilla. She noted that gorillas consume diets that, while primarily folivorous, are quite tough in comparison to large fruits and require much more incisal preparation. This diet includes low quality herbs, bast, and pith. The purpose of her study was to compare patterns of incisor wear in order to determine which diet caused more wear damage to the incisors and to establish whether incisor breadth has an impact on the rates of crown reduction in the two species. She predicted that processing leaves and stems is more destructive to incisors than processing fruits.

In her assessment of incisor wear, McCollum (2007) divided her specimens into four Molar Wear Stages (MWSs), which were differentiated based on the amount of dentin exposure. She measured the Percentage Crown Height Remaining (%CHR) of both upper and lower central and lateral incisors for each specimen in each stage. Original crown height was defined as the average crown height in a sample of unworn juvenile incisors. She used a Mann-Whitney U test to evaluate the significance of %CHR differences between the two species.

The results of the incisor wear analysis were that at all MWSs, measurements of incisor crown reduction were greater in gorillas than in chimpanzees, but only at MWS 4 were those measurements significantly greater. Measurements of %CHR at MWS 4 ranged from 24-51% in gorillas compared to 60-75% in chimpanzees. Overall, wear on both the maxillary and mandibular central incisor was more extensive than on the lateral incisors in both jaws and %CHR was less in the maxilla than in the mandible.

In order to compare incisor breadth, McCollum (2007) used three measurements: (1) length of maxillary and mandibular incisor rows (linear distance from left to right lateral incisor distal margins), (2) maximum mesio-distal lengths, and (3) maximum

crown heights. The first of those measurements was from a sample of dentally mature specimens and the latter two measurements were taken from a sample of unworn juveniles. She also took measurements of maximum mesio-distal lengths and bucco-lingual breadths of the first and second molars because incisor size is often studied relative to molar size. She then plotted incisor row length against estimates of body size (using bitympanic breadth) and compared body-sized adjusted, sex-specific means of incisor breadths and molar areas. Results showed that the incisor rows of gorillas were relatively shorter than those of chimpanzees, especially in the mandible. There was little variation in size-adjusted measures of breadth between the two species.

McCollum (2007) concluded that gorillas' greater reduction in incisor crown height resulted from the greater quantity of food and to the toughness and abrasiveness of the foods gorillas consume compared to those consumed by chimpanzees. This supports the hypothesis that a leafy, pithy diet causes more damage to incisors than a frugivorous diet, but she suggested that further studies are needed in order to test the relationship in other anthropoid taxa. The results of the incisor breadth analysis suggest that crown breadth does not have much, if any, effect on the rate of incisor wear, contrary to Hylander's (1975) conclusion. Some other aspect of incisor morphology may be at play here, such as enamel thickness (Pampush et al., 2012) or crown height (Plavcan and Ruff, 2008).

Ungar (1994a) also presented dietary information that contradicted Hylander's (1975) conclusions. He hypothesized that anterior tooth use differed among species eating foods with different material properties and tested whether, and how, methods or degree of use differed among primates and whether these differences could be explained

by food preferences. He gathered 1784 hours of feeding behavior data and food material property data for *Hylobates lar*, *Macaca fascicularis*, *Pongo pygmaeus*, and *Presbytis thomasi* living sympatrically at Ketambe Research Station in Sumatra. Feeding behaviors were placed into one of six categories based on anterior tooth use: (1) no anterior tooth use, (2) nipping, (3) incising (leaf incising was further subdivided depending on the number of layers of leaves), (4) crushing, (5) scraping, and (6) stripping. Foods were categorized as fruits, leaves, arthropods, or other items. Fruit size, ripeness, pH, pericarp type, seed number, and skin/husk hardness were recorded, as were leaf maturity and size, arthropod type, and characteristics of other foods. He compared feeding behaviors and food types across taxa and found that preferred methods of ingestion differed for foods in different categories and for foods with different material properties.

Results indicated that the species varied in their methods of anterior tooth use when processing (or not processing) fruits, leaves, arthropods, and flowers but not stems. Further, there was intraspecific consistency in the methods used for each food type. The degree of incisor use also depended on the characteristics of each food type. Large fruits required more incisal preparation than small or medium sized fruits. All taxa engaged in more incisal preparation of foods of moderate pH values compared to those with particularly low or high pH values. Hard fruits required more incisal preparation than soft fruits and all taxa rarely used incisors when ingesting soft fruits. Methods of leaf ingestion increased in complexity with size and maturity. Larger arthropods required greater incisor use than small arthropods, which were usually popped into the mouth.

There were also species-specific differences in feeding behavior and food preference. *H. lar* used incisors the least of the four species when ingesting foods, but

when they did, nipping was a common behavior. Preferred foods for *H. lar* were small, ripe, fleshy fruits. *M. fascicularis* utilized incisors more often during ingestion than the gibbons but less so than the other two taxa. Preferred foods were small fruits, though medium and large fruits were sometimes consumed and were ingested via scraping or crushing. *P. thomasi* used their incisors more frequently, incising the majority of fruits and leaves consumed, but also engaging in more complex incisor use when feeding on tougher or harder foods. Leaves of all sizes and maturity were consumed and were the food of preference. More complex feeding behaviors were utilized for the larger and more mature of those leaves. *P. pygmaeus* used anterior teeth, and lips, more than any other species and for almost all food consumed. Frequently eaten foods were large and hard fruits, mature leaves, and woody stems.

These results showed that at least some of the differences in incisor use among taxa could be attributed to dietary differences and that fruits do not necessarily require higher degrees of incisal preparation than leaves or herbaceous foods, as Hylander (1975) suggested. Leaves actually required a broader range of incisal preparation and the taxon that ate the most leaves used incisors more often than two more frugivorous taxa. Overall, foods that were large, hard, or mature (tough) involved greater degrees of incisal contact during ingestion.

Ungar (1994b) used a sample of specimens of the same Sumatran primate species to investigate incisor microwear. He used a scanning-electron microscope (SEM) to analyze the labial, lingual, and incisal surfaces of maxillary and mandibular central incisors. He compared the ratio of pits to scratches and also dentin exposure and calculus build-up among species.

Results revealed differences among taxa in microwear features. *P. pygmaeus* and *P. thomasi* showed more prism exposure than *H. lar* or *M. fascicularis*. *H. lar* had more calculus on the incisors than any other species and, in general, calculus build-up was greater on the lingual surfaces of both upper and lower incisors in all species. *H. lar* also had less pitting than any other taxon and fewer scratches than any other taxon, though scratches tended to be broader on the I^1 lingual surface. *P. pygmaeus* had broader scratches on the I^1 lingual surface. In general, scratches appeared to occur in higher densities on I^1 than I_1. There were no differences in scratch orientation among the species.

H. lar (diet of small, ripe, soft, fleshy fruits and use little or no incisal preparation) showed little enamel prism exposure, substantial calculus on both lingual and labial surfaces, and few pits and scratches. *M. fascicularis* (diet of mostly small, fleshy fruits, though they eat a wide range of foods, and only occasionally engage in complex incisal preparation) also showed little enamel prism exposure but had considerably less calculus than the gibbons. Densities of pitting were relatively higher. *P. pygmaeus* (diet of mostly fruits but also eat a wide variety of other foods, often engaging in complex anterior tooth use) showed greater prism exposure, had calculus build-up along the lingual surfaces, and had much greater densities of scratches, compared to the other species, that were relatively broad. *P. thomasi* (diet of mostly leaves and often use incisors to process thick bunches of leaves or tough fruit husks) showed considerable prism exposure but not calculus build-up. Scratch densities were high but scratches were lower in breadth, and there was significant pitting on incisal surfaces.

These results suggested that differences between taxa were due to diet and ingestive behaviors. Enamel prism exposure is associated with the number of etching reagents in the diet (i.e. percentage of mature leaves and unripe fruits); calculus build-up is associated with the lack of incisal preparation; scratch density represents the abrasiveness of the diet; scratch breadth may reflect the amount of grit in the diet and therefore the height of substrate during feeding; and scratch orientation reflects the direction of food movement across the teeth.

Ang et al. (2006) developed a model for understanding incisor orientation and the forces that affect incisor efficiency. In order to do this, they attempted to show how, for a food item of any given toughness, the forces required for the incisors to fracture the item depend on the form of the incisor tip, its orientation to the surface of the item, and the friction between the incisor and the food surfaces. They assume that incisor crowns adapt to reduce the effects of toughness and energy-dissipating mechanisms (i.e., friction and plastic deformation) of food items, minimizing the work or forces required to fracture foods. Prior to this study it was thought that incisors were most efficient when the long axis of the tooth is parallel to the direction of force applied by the incisor to an object, implying that food items fracture due to compressive stress. The authors test this by modeling the incisor as a wedge, ignoring curvature, with the labial and lingual surfaces as the sides of the wedge. The angle formed by the sides of the wedge was termed the apex angle and the axis bisecting the apex of the wedge was termed the apex bisector.

Taking contact force, frictional force, and the force that resists fracturing into account, they created a model from which they determined that the external force required during incision is dependent on the friction coefficient, the tilt angle, and the

apex angle. For every combination of friction coefficient and apex angle, there is a tilt angle at which the work required to fracture an object is least (Figure 9). This tilt angle may or may not be in the direction of the applied force, as previously thought.

This information was applied to a sample of human maxillary and mandibular central incisors (though it can be applied to any species with wedge-shaped incisors). The average apex angle was 34.0° for the maxillary incisors and 24.0° for the mandibular incisors. The angle between the long axis and the apex bisector was 14.0° for maxillary incisors and 11.5° for the mandibular incisors. If the coefficient of friction between human teeth and the food item eaten is known, then it is possible to determine optimal tilt angle for maxillary and mandibular incisors. Data on the coefficient of friction for different food types is rare but tilt angles were estimated based on a coefficient range of 0.1 – 0.6.

This model shows that optimal tilt angle of incisors is diet dependent, but on the coefficient of friction, rather than on material properties such as toughness. The coefficient of friction is rarely measured so it is not possible to determine optimal tilt angle of incisors for most species at this point. The authors argue that toughness determines the basic level of work required for incision by the muscles. Work above this minimum depends on the shape and orientation of the incisors. A low coefficient (0.1 – 0.3) of friction means the optimal tilt angle for human maxillary incisors is 27.0 – 34.0° and for mandibular incisors, 32.0 – 39.0°. A higher coefficient of friction (0.4 – 0.6) means the optimal orientation for upper incisors is the apex bisector is parallel to the direction of the force, and a tilt angle of 23.0 – 29.0° is best for lower incisors.

Because the orientation of the incisors should result in the greatest energy savings, wear should cause a decrease in efficiency. The authors conclude that incisors should be oriented at tilt angles optimal for the highest values of coefficients of friction. This conclusion does not support earlier explanations of tooth orientation, but rather suggests that those explanations are possible only under certain conditions. Hard diets would require more robust incisors. Increasing robusticity may mean having broad incisors with large apex angles and 0° optimal tilt angles. Incisors with smaller apex angles would have non-zero degree optimal tilt angles. There is a trade-off between having very strong incisors (larger apex angles, broader teeth) and having incisors that wear less rapidly, remaining sharp (smaller apex angles). The range of apex angles across the primate order should be explored with respect to physical properties of diets. Further, orientation of the incisors should be compared with data on the movements of the head and mandible during ingestion.

Plavcan and Ruff (2008) conducted a study on canine bending strength, the methods of which could potentially be applied to incisors. They measured, in a large sample of anthropoids and strepsirrhines and in a sample of carnivores, body mass (based on skull length), canine crown height, mesio-distal length, and bucco-lingual breadth. Canine bending strength about the mesio-distal and bucco-lingual axes was determined using equations that model the canine as a beam, thus assessments of strength apply to resistance at the base of the tooth when bending forces are applied to the tooth crown. The authors assumed that the canine has an approximately elliptical cross-section and that canine shape is similar among all taxa.

In terms of body mass, skull dimensions, tooth dimensions, and bending strength, all primates were compared to carnivores and among the primates, anthropoids and strepsirrhines were compared (to account for shape differences between the latter two groups). Plavcan and Ruff (2008) found that primates showed greater variation in canine shape than carnivores, and that primate canines get taller as they get bigger in occlusal dimensions, while carnivore canines get shorter. Strepsirrhines tended to have to greatest mesio-distal elongation in cross-section, while carnivores had the least and anthropoids were intermediate, but these results were not significant and were possibly due to phylogeny.

In terms of size, relative to body mass and skull length, primate canines tended to be larger because of the relatively longer skulls of carnivores. Primates, and especially anthropoids, tended to have as large or larger relative canine size than carnivores. When relative strength was compared, primates showed greater canine strength than carnivores of similar size, though results were not significant. There was also no significant difference in canine strength between males and females. Bending strength was greater in shorter canine crown heights for primates and primate canines were stronger relative to crown height compared to carnivores. Primate behavior was also taken into consideration by comparing canine size and strength among primates with different social systems. More polygynous species, compared to monogamous or polyandrous species, had greater male canine size and strength.

The authors explained that few primate species are known to use their canines to open hard objects. These primates showed considerably greater canine strength in both mesio-distal and bucco-lingual dimensions than those who do not engage in this feeding

behavior. Carnivorous primates *Pan* and *Papio* did not show significantly strong canines so there was no association between canine strength and processing meat.

The results suggest that among canines of identical shape, the larger ones are stronger. Of canines equal in occlusal dimensions, the shorter ones are stronger. The fact that some primates use their canines to open hard objects, and that these primates have stronger canines, suggests that canines can be modified for strength when selective pressure for opening such hard objects is present, regardless of phylogenetic associations.

This study has potential implication for understanding incisor strength in relation to diet as incisors can be measured and compared in similar ways. Whether or not there is a relationship between bending strength and degrees of mesio-distal and labial curvature would be of particular interest. Further, the relationship between incisor strength and diet may be less complicated by social behavior compared to canines, as incisor morphology may be less influenced by sexual selection than canines in some primate species. Perhaps the relationship between incisor bending strength and diet could also be better understood with the use of models like the one developed by Ang et al. (2006). Such models could potentially take into consideration mesio-distal and labial curvature.

The Future for Incisor Studies

While the above-mentioned studies have investigated different aspects of primate incisor morphology, there is still much we do not understand about the nature of incisor function. Much of the necessary dietary and behavioral data to further our understanding have not been collected for most primate species. Also, the manner in which morphology is associated with diet needs to be reconsidered. Many diet-tooth morphology studies continue to examine morphology within the contexts of frugivore/folivore, hard-

object/soft-object dichotomies, or other similarly broad categories, including the present study and several of those discussed above, though Ungar (1994a,b) and Ang et al. (2006) attempted to address these problems by taking into consideration different physical properties of foods. These categories may be meaningless because (1) they may not reflect aspects of diet that actually influence selection for morphology, (2) different taxa may have developed different morphological solutions to similar problems and this may not be reflected within the context of broad categories, and (3) behavioral solutions to biomechanical challenges may not be recognized (McGraw and Daegling, in press).

The study of dental morphology needs to be refocused and emphasis should be placed on interpreting morphological features within the context of specific physical properties of foods and how teeth are used to process them, rather than by the type of food on which primate species predominately feed. Further, these features should be separated from taxonomic associations to account for intraspecific dietary and behavioral variation that may occur among different populations. One of the purposes of gaining an understanding of functional morphology is to be able to make inferences about diet and feeding behavior in fossil taxa. Until this shift in focus takes place, and until data on the material properties of foods are available, it may not be possible to accurately infer these aspects of ecology in the fossil record.

Conclusion

The present study suggests no association between diet categories and incisor curvature in a sample of cercopithecids, contradicting the results found by Deane et al. (2005) and Deane (2009a,b, In press) in hominoids and platyrrhines. There are several

possible reasons why this sample of cercopithecids does not show the same association, including unequal samples in each category and differences in methodology. Further research will attempt to eliminate these potential problems. The issue of greater concern is that this study, as well as those on which it builds, classify taxa into broad dietary categories in the attempt to make associations between morphology and function, likely overlooking the aspects of diet that actually apply selection pressures on tooth form.

The functional mechanism for variation in incisor curvature is unknown and will remain so until functional morphologists can study tooth form separately from broad dietary categories and taxonomy, keeping interspecific and intraspecific variation in diet and behaviors into account, and reflecting the material properties (e.g., toughness, hardness, friction coefficients). Investigating this relationship correctly in cercopithecids and other primate taxa could have important implications for understand the feeding ecology of fossil primates, but it would be unwise to apply information that does not account for the full range of variation in the primate diet or for the specific physical properties of foods to the fossil record.

Figures and Tables

Figure 1. The three stages of the HR-PCF method: left, digital image of a phalanx; center, image reduced to a grey-scale outline and represented by thousands of pixels; right, identifying discontinuities in the curvature, points of inflection, and the endpoints of the curve (done automatically using software specifically designed for HR-PCF). From Deane et al. (2005).

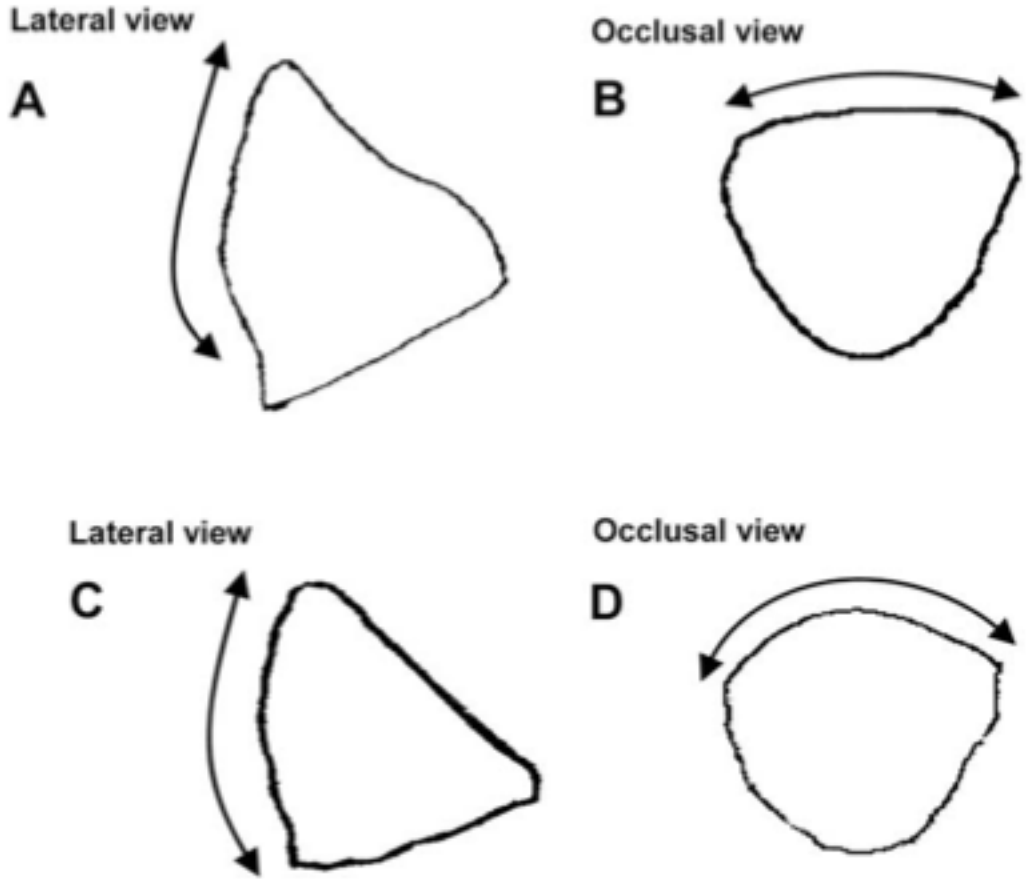


Figure 2. Upper central incisors showing differences in curvature: (A) the flatter labial curvature and strongly angled curvature superior to the cervical line characteristic of *Gorilla gorilla beringei* and the other dedicated folivores and mixed folivore/frugivores; (B) the moderate mesio-distal curvature in *Gorilla gorilla beringei*, a folivore; (C) the uniform curvature characteristic of *Pan troglodytes* and all frugivores; (D) the significant mesio-distal curvature in *Pan troglodytes*, a frugivore.

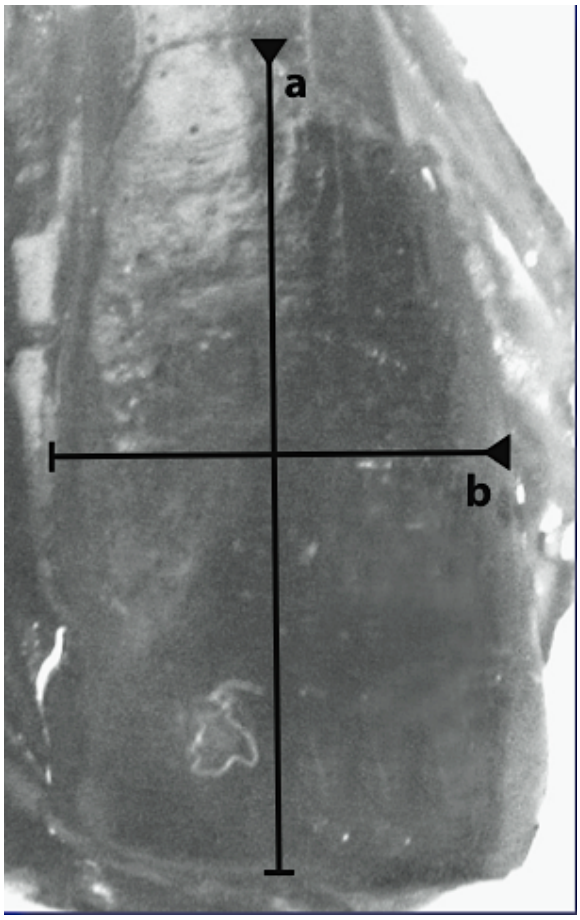


Figure 3. *Papio anubis* central incisor. a) labial curve measuring from the center of the cemento-enamel junction (CEJ) to the center of the incisal edge; b) mesio-distal curve measuring from the midpoint (total length from CEJ to incisal edge/2) of the mesial edge to the midpoint of the distal edge.

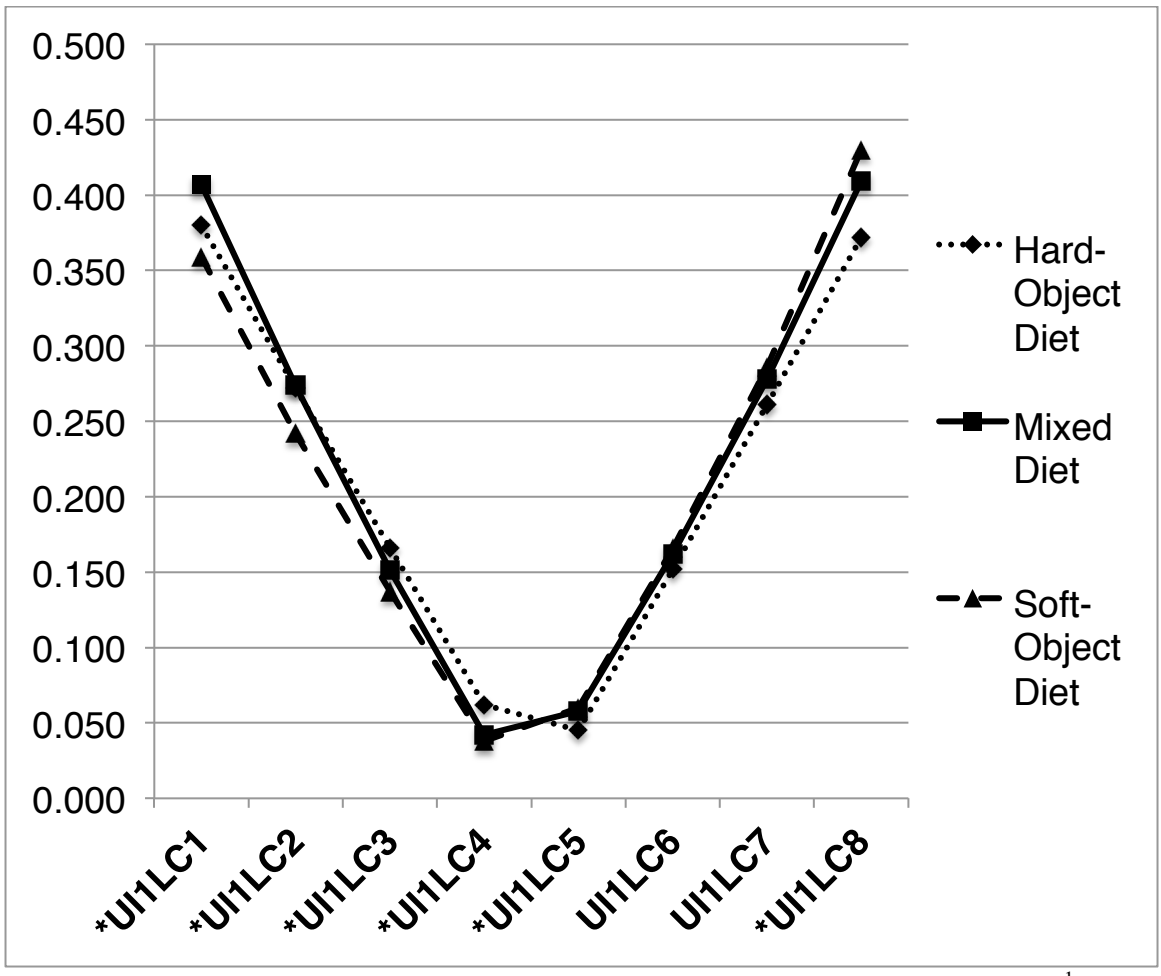


Figure 4. Comparison of the mean slopes for each group at each point on the I^1 labial curve.

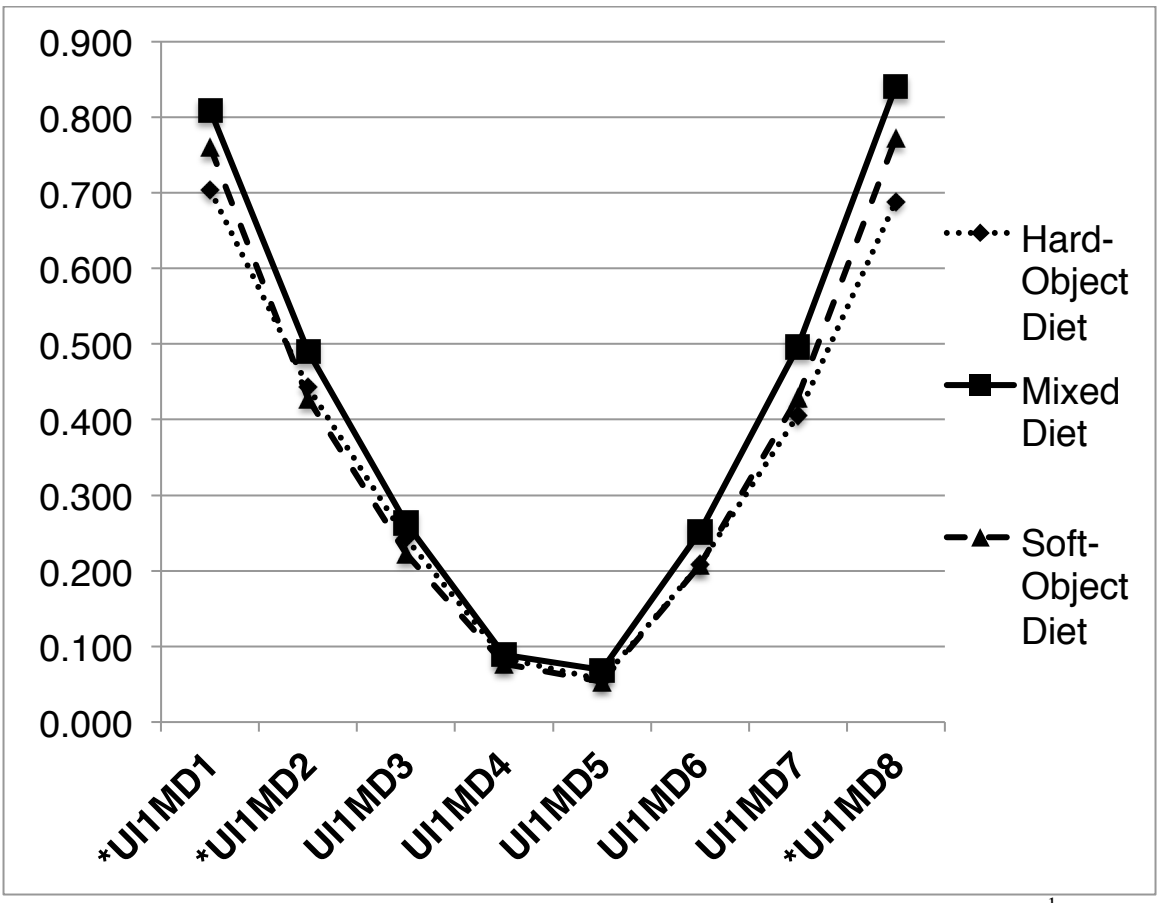


Figure 5. Comparison of the mean slopes for each group at each point on the I^1 mesio-distal curve.

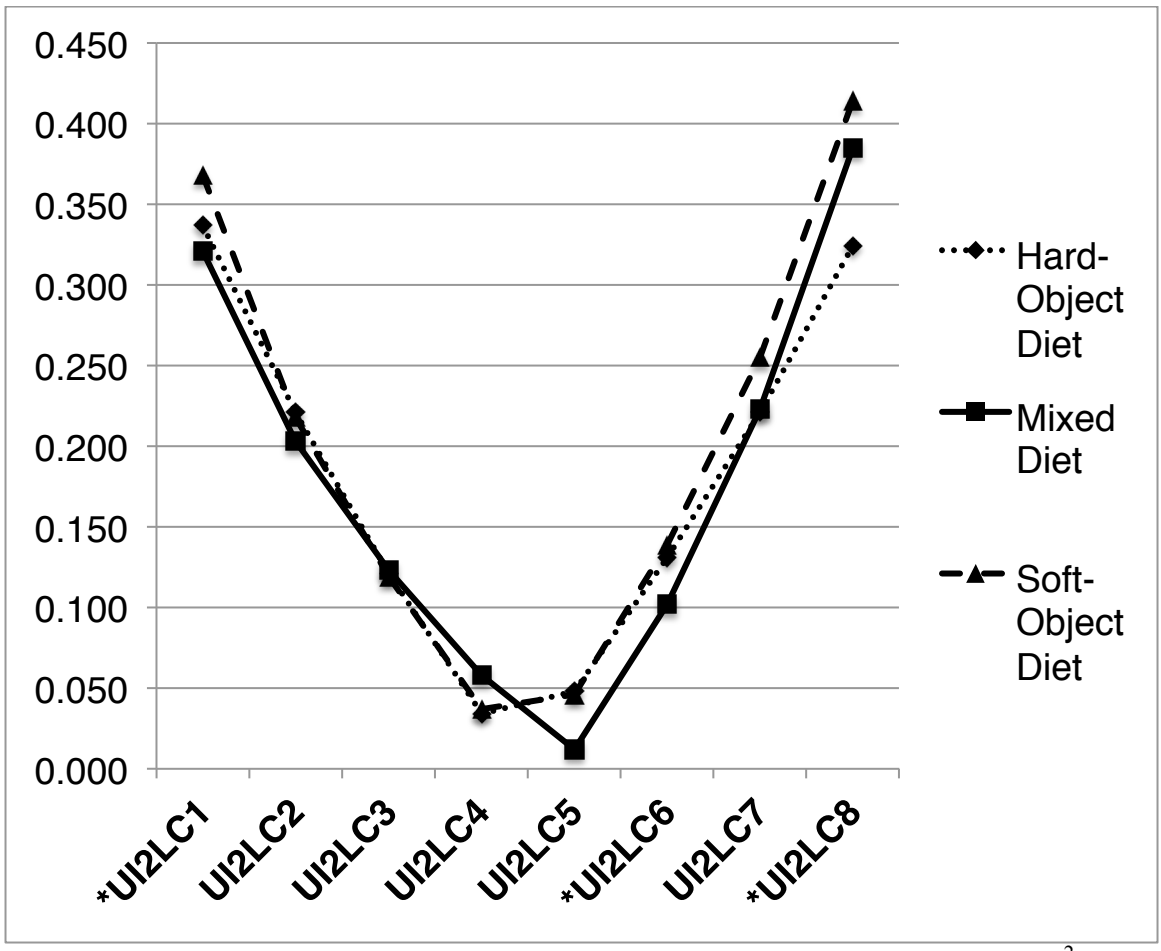


Figure 6. Comparison of the mean slopes for each group at each point on the I^2 labial curve.

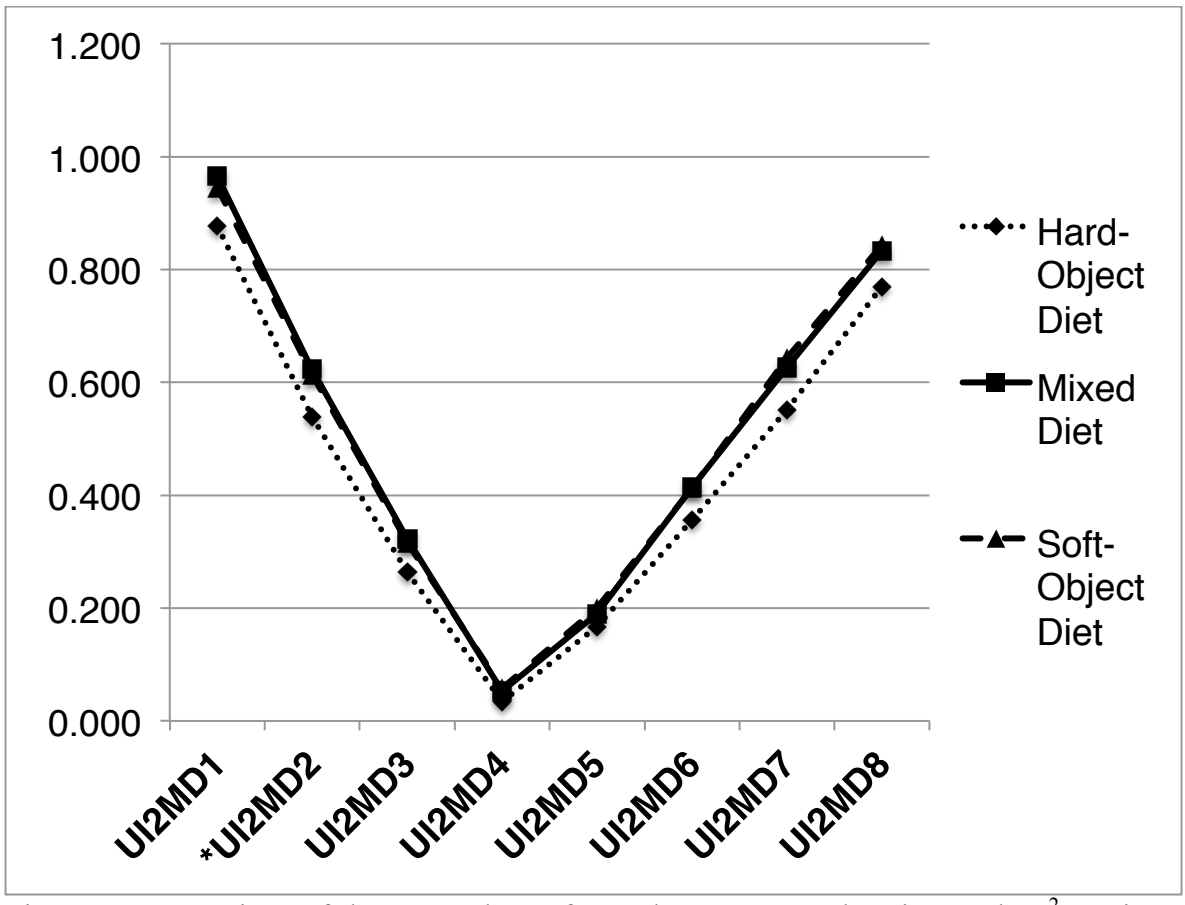


Figure 7. Comparison of the mean slopes for each group at each point on the I^2 mesio-distal curve.

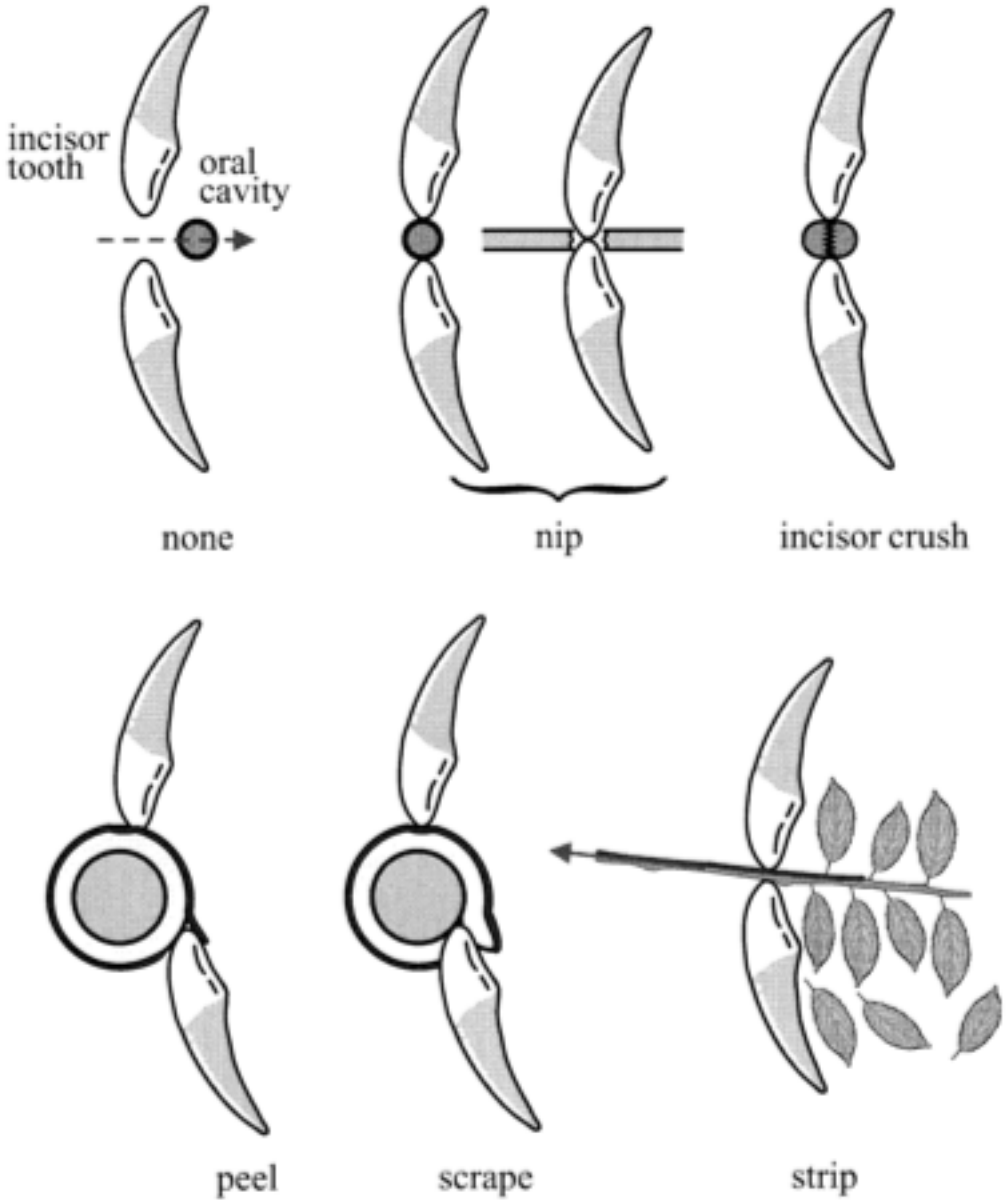
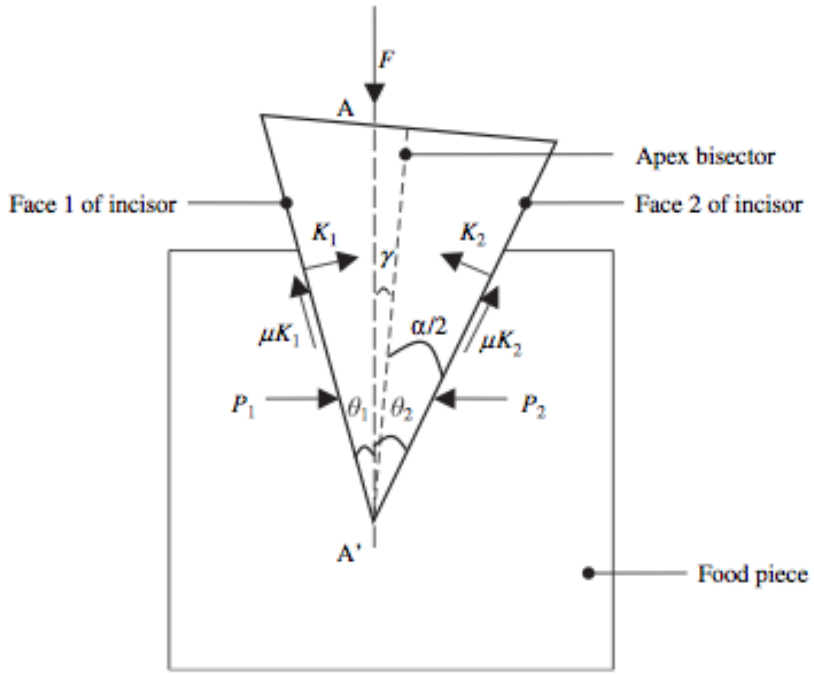
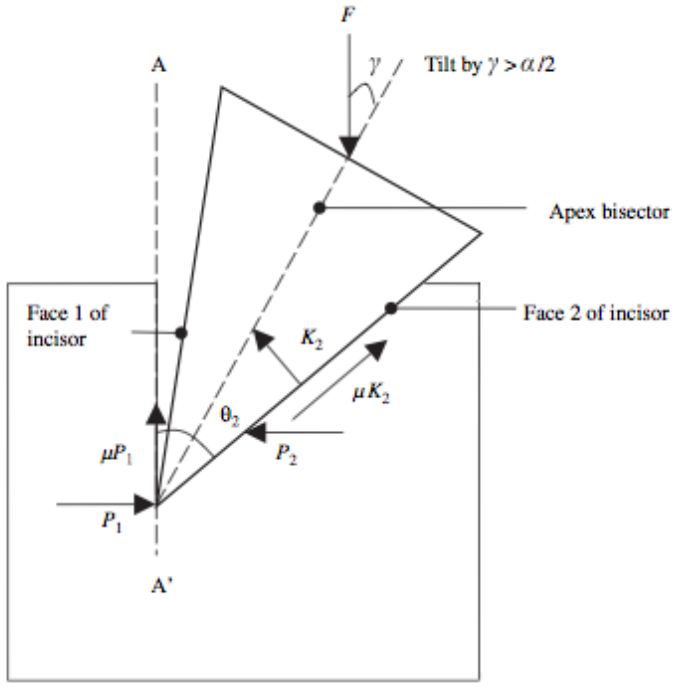


Figure 8. Modes of ingestion used by primates. Nipping and crushing crack foods; peeling, scraping, and stripping grip foods. From Agrawal and Lucas (2003).



A



B

Figure 8. (A) The incisal tip, modeled as a wedge, being driven into a block. The angle bisector and direction of applied force *F* form a small tilt angle γ. (B) A larger tilt angle. From Ang et al. (2006).

Species	N=Male	N=Female	Total
Group 1 (hard-object)			
Cercocebus torquatus	10	7	17
Macaca nemestrina	9	14	23
Group 2 (mixed)			
Lophocebus albigena	11	4	15
Papio anubis	7	10	17
Procolobus badius	7	10	17
Group 3 (soft-object)			
Cercopithecus mitis	13	14	27
Chlorocebus aethiops	16	14	30
Erythrocebus patas	8	4	12
Nasalis larvatus	5	3	8
Trachypithecus cristatus	11	11	22
Total: 10 species	**97**	**91**	**188**

Table 1. Distribution of the specimens.

Groups compared	Points of mean slopes with greatest differences between groups
1 and 2	I^1 labial: 3, 5, 8 I^1 mesio-distal: 8
2 and 3	I^1 labial curve: 2 I^1 mesio-distal: 2 I^2 labial: 6, 8
1 and 3	I^1 labial: 1, 4, 8 I^1 mesio-distal: 1, 8 I^2 labial: 1, 6

Table 2. Mean slopes of greatest variation.

Groups compared	Percentage of correct assignment
1 and 2	77.3%
2 and 3	73.4%
1 and 3	74.6%

Table 3. Logistic regression analysis results.

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